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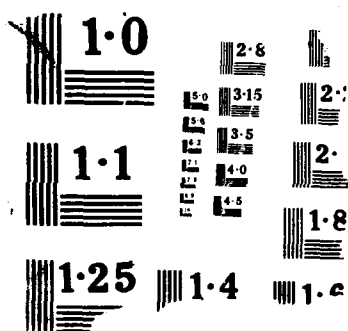
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AQUATIC PLANT CONTROL
RESEARCH PROGRAM

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INTERACTIONS BETWEEN MACROPHYTE GROWTH
AND SEDIMENT NUTRIENT AVAILABILITY

by

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<p>Aquatic macrophytes rely primarily on sediment as a direct source of nitrogen (N) and phosphorus (P). The availability of these nutrients in sediments is affected markedly by sediment type, and is also influenced by macrophyte growth. On sediments planted with <i>Hydrilla verticillata</i> (L.f.) Royle compared with control (unplanted) sediment, reductions of >90 percent and >30 percent in concentrations of exchangeable N and extractable P were measured during two 6-week periods of growth. Diminished N availability in sediments due to uptake by <i>Hydrilla</i> resulted in nutrient limitation of subsequent <i>Hydrilla</i> growth. Concomitant increases (>30 percent) in the concentration of exchangeable potassium (K) suggest that this element, obtained via foliar uptake from overlying water, may be exchanged by macrophyte roots for ammonium in sediment. Exchange of K for ammonium in sediments occurred only under conditions of N limitation in this species.</p> <p style="text-align: right;">(Continued)</p>					
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19. ABSTRACT (Continued).

Changes in sediment nutrient availability effected by *Hydrilla* in this investigation appear to have been entirely a function of nutrient uptake, since this species had a minimal influence on sediment redox potential. In contrast, the emergent macrophyte *Sagittaria latifolia* Willd. effectively promoted sediment oxidation via oxygen evolution from its roots. Species such as *Sagittaria*, which can modify sediment redox potential, may have an effect on sediment nutrient composition exceeding that due to nutrient uptake alone.

Variations in the abilities of different aquatic macrophyte species to deplete sediment nutrients and to contend with autogenic reductions in nutrient availability may have an important influence on successional development in aquatic macrophyte communities. Changes in sediment chemistry induced by aquatic macrophytes, in addition to influencing subsequent nutrient availability, also potentially affect element exchanges with overlying water.

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PREFACE

The studies reported herein were sponsored by the Department of the Army, Office of the Chief of Engineers (OCE), Directorate of Civil Works (DAEN-CW), through the US Army Corps of Engineers Aquatic Plant Control Research Program (APCRP). Funds were provided by DAEN-CW under Department of the Army Appropriation No. 96X3122 Construction General. The APCRP is managed by the US Army Engineer Waterways Experiment Station (WES), Vicksburg, Miss. Technical Monitor for OCE was Mr. E. Carl Brown. Principal investigator for these studies was Dr. John W. Barko, Environmental Laboratory (EL), WES. Experimental design, data analysis, and interpretation were provided by Drs. Barko, R. Michael Smart, and Rex L. Chen. The report was prepared by Dr. Barko. Reviews of this report were provided by Dr. Thomas L. Hart and Mr. William D. Taylor of the EL. Additional reviews were provided anonymously by members of the editorial boards of the journals Aquatic Botany and Freshwater Ecology. Technical assistance was provided by Ms. Dwilette G. McFarland, Mr. James Conley, Ms. Avis Howell, and Mr. Arthur Miller of the EL. The report was edited by Ms. Jessica S. Ruff of the WES Information Technology Laboratory.

This investigation was performed under the general supervision of Dr. John Harrison, Chief, EL, and Mr. Donald L. Robey, Chief, Ecosystem Research and Simulation Division, and under the direct supervision of Dr. Thomas L. Hart, Chief, Aquatic Processes and Effects Group. Manager of the APCRP was Mr. J. Lewis Decell, EL.

COL Dwayne G. Lee, CE, was the Commander and Director of WES. Dr. Robert W. Whalin was Technical Director.

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INTERACTIONS BETWEEN MACROPHYTE GROWTH AND
SEDIMENT NUTRIENT AVAILABILITY

PART I: INTRODUCTION

1. Considerable effort has been directed toward examination of the nutrition of rooted submersed macrophytes (refer to reviews of Sculthorpe 1967; Denny 1980; Smart and Barko 1985; Agami and Waisel 1986; Barko, Adams, and Clesceri 1986). Rooted submersed macrophytes are unique in having access to nutrients both in the sediment via root uptake and in the open water via foliar uptake. While some controversy persists regarding the role of roots versus shoots in the overall nutrition of these plants (cf. Agami and Waisel 1986), it is generally accepted that under most circumstances sediments are an important source of nutrients, particularly nitrogen (N) and phosphorus (P) (Nichols and Keeney 1976, Barko and Smart 1981a, Carignan 1982, Smith and Adams 1986). Since losses of these nutrients and others during senescence and decomposition can be quite large (e.g., Carpenter 1980), there is a potential for nutrient reserves in sediments to become depleted.

2. Limited evidence from field studies indicates that reductions in N and P concentrations can occur within the root zones of submersed macrophytes (Prentki 1979, Carignan 1985). These reductions have been ascribed both to nutrient uptake by rooted macrophytes and to altered sediment redox potential (Jaynes and Carpenter 1986). Macrophyte roots influence sediment redox potential by transporting oxygen produced in shoots to sediment (Sculthorpe 1967). Since changes in sediment redox potential can affect the availability of nutrients, the magnitude of oxygen release by macrophyte roots may have an important effect on nutrient availability to aquatic macrophytes. The extent to which changes in sediment nutrient composition are effected either directly (due to nutrient uptake) or indirectly (due to change in sediment redox potential) by macrophytes and the degree to which such changes might affect subsequent plant growth have not been evaluated.

3. In the laboratory culture facilities at the US Army Engineer Waterways Experiment Station (WES), the authors have frequently observed diminished growth of submersed macrophytes on repeatedly planted sediments, suggesting progressive nutrient limitation as a possible growth-retarding factor (Smart and Barko 1985). An important implication of these findings in

combination with those cited above is that, under some circumstances, aquatic macrophyte growth may be self-limiting. In view of this possibility, the objective of this investigation was to evaluate interrelationships between submersed macrophyte growth, sediment redox potential, and concentrations of N, P, and potassium (K) in sediments. The authors chose to examine these interrelationships in *Hydrilla verticillata* (L.f.) Royle, an adventive submersed macrophyte species with a worldwide distribution (Cook and Luond 1982). For comparative purposes in studies of sediment redox potential, *Sagittaria latifolia* Willd., an emergent aquatic macrophyte, was also included.

PART II: MATERIALS AND METHODS

Experimental Design

4. A principal study was designed to allow comparisons of *Hydrilla* growth on previously planted and previously unplanted sediment; this study was conducted in two phases with a duration of 6 weeks each (Figure 1). During the pretreatment phase, six 1-l containers of fine-textured Brown's Lake sediment (characterized in McFarland and Barko, in press) were planted, while another 12 1-l containers of the same sediment remained unplanted under otherwise identical environmental conditions. After 6 weeks of growth, aboveground biomass of *Hydrilla* was removed from planted containers by clipping at the sediment surface, and rootstocks were gently pulled from the sediment. At that time (beginning of experimental phase), the six previously planted containers were replanted with *Hydrilla*, six of the previously unplanted containers were planted, and the remaining six containers were again retained in an unplanted (control) condition. Results reported herein derive from the experimental phase of study (Figure 1) in which there were two treatments (previously planted and previously unplanted sediments) and a control (unplanted sediment).

5. A related secondary study was conducted on fine-textured Lake Washington sediment (characterized in Barko and Smart 1983) to examine the relationship over time between N status of *Hydrilla* shoots and K concentration in sediment (rationale provided later in text). In this study there was a single treatment (planted sediment) and a control (unplanted sediment).

6. Another secondary study involving *Hydrilla* and *Sagittaria* was conducted on Brown's Lake and Lake Washington sediments to examine interrelationships among macrophyte growth, sediment redox potential, and sediment nutrient composition (rationale provided later in the text). Profiles of sediment redox potential were measured with platinum electrodes, coupled with a calomel reference electrode according to procedures described in Chen and Barko (in press). In this study there were two treatments (sediment planted with *Hydrilla* and sediment planted with *Sagittaria*) and a control (unplanted sediment). In all studies described herein, control sediments served in evaluating relative effects of macrophyte growth on sediment chemistry.

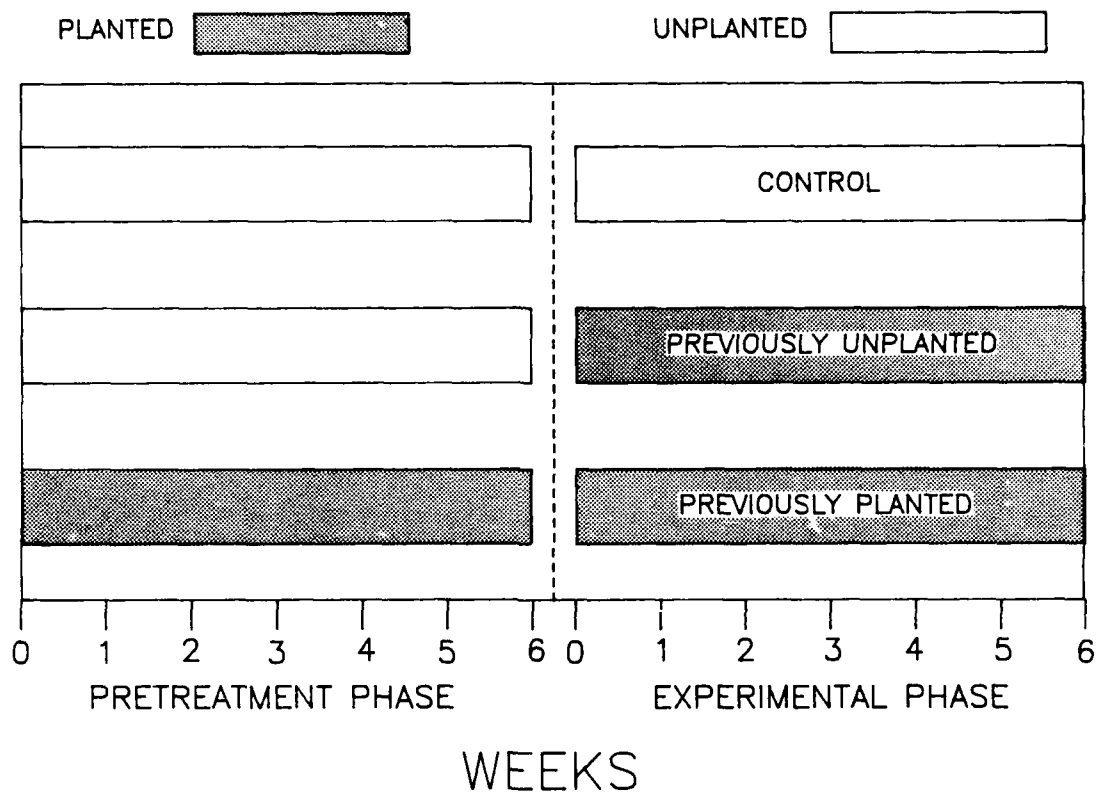


Figure 1. Experimental design. Study was conducted in two phases: pretreatment and experimental. Data are reported for the experimental phase, during which there were two treatments (previously planted and previously unplanted sediments) and a control (unplanted sediment)

Experimental Environment and Procedures

7. Studies were conducted in the controlled environment facilities of the Environmental Laboratory, WES (Barko and Smart 1980, 1981b). Water temperature was maintained at 24° C, and light was provided at moderate levels (500 to 1,000 $\mu\text{E}/\text{m}^2/\text{sec}$) during 12- to 14-hr photoperiods. The solution used in these studies was identical to that described in Table 1 of Smart and Barko (1985). In summary, the solution contained major nutrients except N and P, which were excluded to minimize confounding effects of algae growth (Smart and Barko 1985).

8. Apical tips of *Hydrilla*, about 15 cm in length, which were obtained from our cultures, were planted uniformly to a sediment depth of 5 cm. For this species, initial plant biomass was approximately 0.15 g dry weight, representing six sprigs per sediment container. *Sagittaria* was planted as tubers (four per sediment container), with an initial mass of 10.2 g per container. Sediment surfaces in both planted and unplanted sediment containers were overlaid with a thin layer of washed silica sand to minimize nutrient exchange with overlying solution. Immediately after planting, sediment containers were placed in the plant growth systems, and solution was added. Solution was exchanged as necessary during studies to minimize changes in water chemistry conditions.

9. Evaluations of macrophyte growth were based on changes in shoot height and oven-dry (80° C) biomass. Root and shoot biomass were determined separately, then summed to calculate total biomass. Shoot biomass was determined for macrophytes in all treatment containers, while root biomass was determined in only half of the containers. Remaining sediment containers were used to determine sediment nutrient concentrations (as described below). Nutrient concentrations in macrophyte shoots were determined following digestion in a mixture of hydrogen peroxide and sulfuric acid (Allen et al. 1974). Nutrient accumulation within shoots was calculated as the product of shoot biomass and shoot nutrient concentration, corrected for contributions of initial propagules.

Analytical Protocol

10. Duplicate 50-ml samples of sediment from containers designated for physical and chemical determinations were removed with a corer. These samples were taken over a depth of about 15 cm, extending from the container surface to its base, then combined for each container by mixing (while avoiding contact with air) in preparation for immediate analysis. Nutrient concentrations in sediment interstitial water were determined following high-speed centrifugation according to procedures provided in Barko and Smart (1986). Extractable P in sediment was obtained by shaking 2 g wet sediment with 25 ml of an extractant containing 0.03 N NH_4F and 0.025 N HCl for 1 min (Olsen and Sommers 1982). Exchangeable ammonium-N and K were obtained by shaking 5 g wet sediment with 50 ml of an extractant containing 1 M NaCl in a modification of the extraction procedure for determining inorganic forms of N (Bremner 1965). The use of NaCl rather than KCl allowed the determination of both exchangeable N and K on a single sediment extract. All extracts were filtered and then acidified with HCl (to pH of ca. 2.0) in preparation for analyses.

11. Analyses of N and P were performed colorimetrically using Technicon Auto-Analyzer II procedures. Potassium was determined by atomic absorption spectrophotometry. Concentrations of extracted nutrients are expressed here on the basis of sediment dry mass following correction for moisture content determined on separate sediment aliquots. Sediment density, determined from the same aliquots, was used in nutrient mass balance calculations. Statistical analyses of data were performed using the Statistical Analysis System. Results reported here as statistically significant were examined at the 5-percent probability level.

PART III: RESULTS

Principal Study

12. Shoot height, as a morphological indicator of growth in *Hydrilla*, was reduced significantly beyond 2 weeks on previously planted sediment in contrast with height on previously unplanted sediment (Figure 2). Differences in shoot height between treatments increased through time, and by 6 weeks, height on previously unplanted sediment was nearly twice as great as that on previously planted sediment. Total biomass production in *Hydrilla* was reduced significantly, by about one third on previously planted sediment compared to previously unplanted sediment (Figure 3). A significant increase in the ratio of root to shoot biomass (2.5-fold) accompanied reduced total biomass production on previously planted sediment.

13. Concentrations of N, P, and K were much lower in *Hydrilla* shoots grown on previously planted sediment than on previously unplanted sediment (Figure 4). Nutrient accumulation in shoots was affected by treatment to a much greater extent than was biomass production. Accumulations of N, P, and K in shoots of plants grown on previously planted sediment were only 26, 26, and 38 percent, respectively, of accumulations on previously unplanted sediment. Despite overall reductions in nutrient accumulation by *Hydrilla* on previously planted sediment, only N concentration was reduced to a critically low level (see subsequent discussion).

14. Growth of *Hydrilla* greatly affected concentrations of extractable sediment nutrients (Figure 5). A single period of growth (previously unplanted sediment) resulted in maximal reduction of exchangeable N, with no further reduction due to an additional period of growth (previously planted sediment). In contrast, a single period of growth resulted in only a minor reduction in extractable P and no change in exchangeable K. However, two periods of growth resulted in a significant reduction in extractable P and a significant increase in exchangeable K. Overall, two periods of growth resulted in 95- and 36-percent reductions in exchangeable N and extractable P concentrations, respectively, and a 32-percent increase in exchangeable K concentration relative to the unplanted control sediment.

15. Changes in nutrient concentrations within the sediment interstitial water essentially paralleled those determined in sediment extracts.

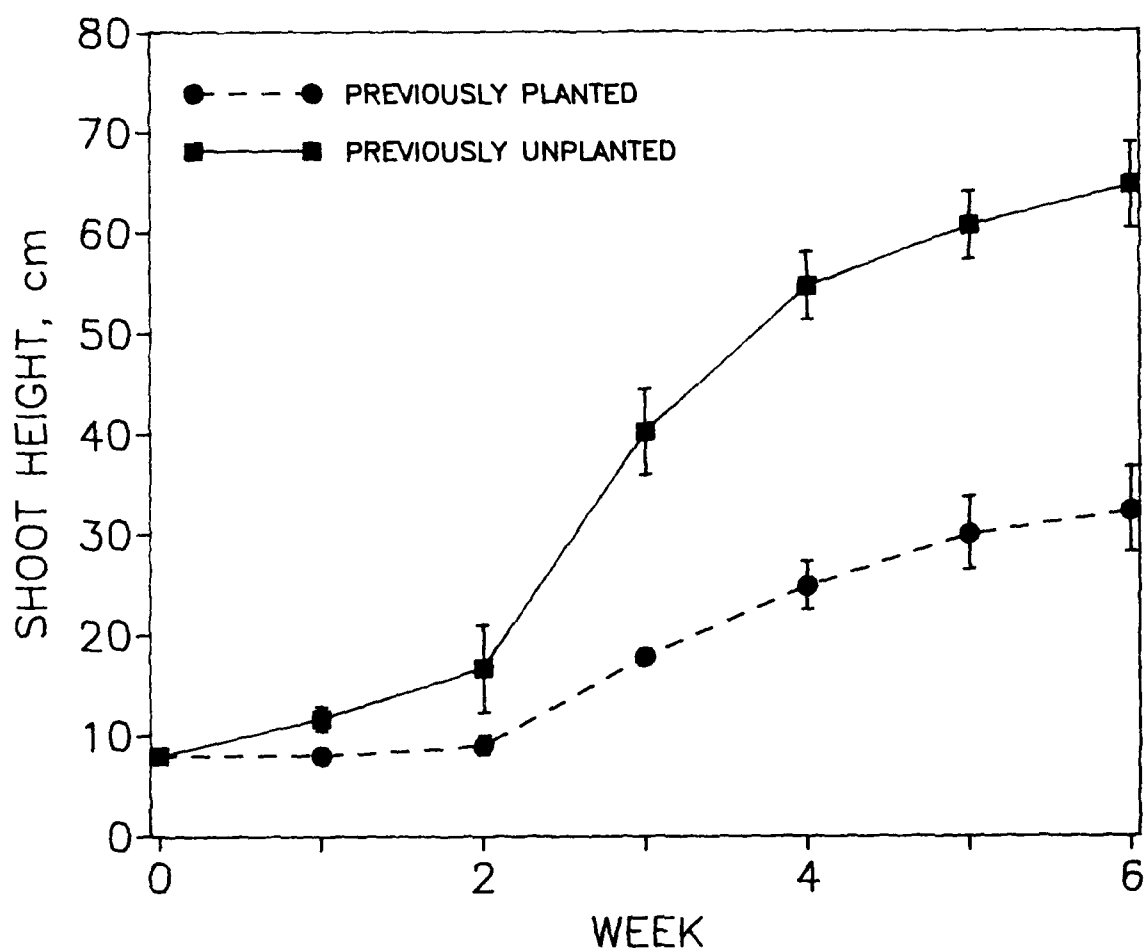


Figure 2. Shoot height in *Hydrilla* grown over a period of 6 weeks on previously planted and previously unplanted sediment. Values of shoot height are means ($n = 6$), with associated standard deviations

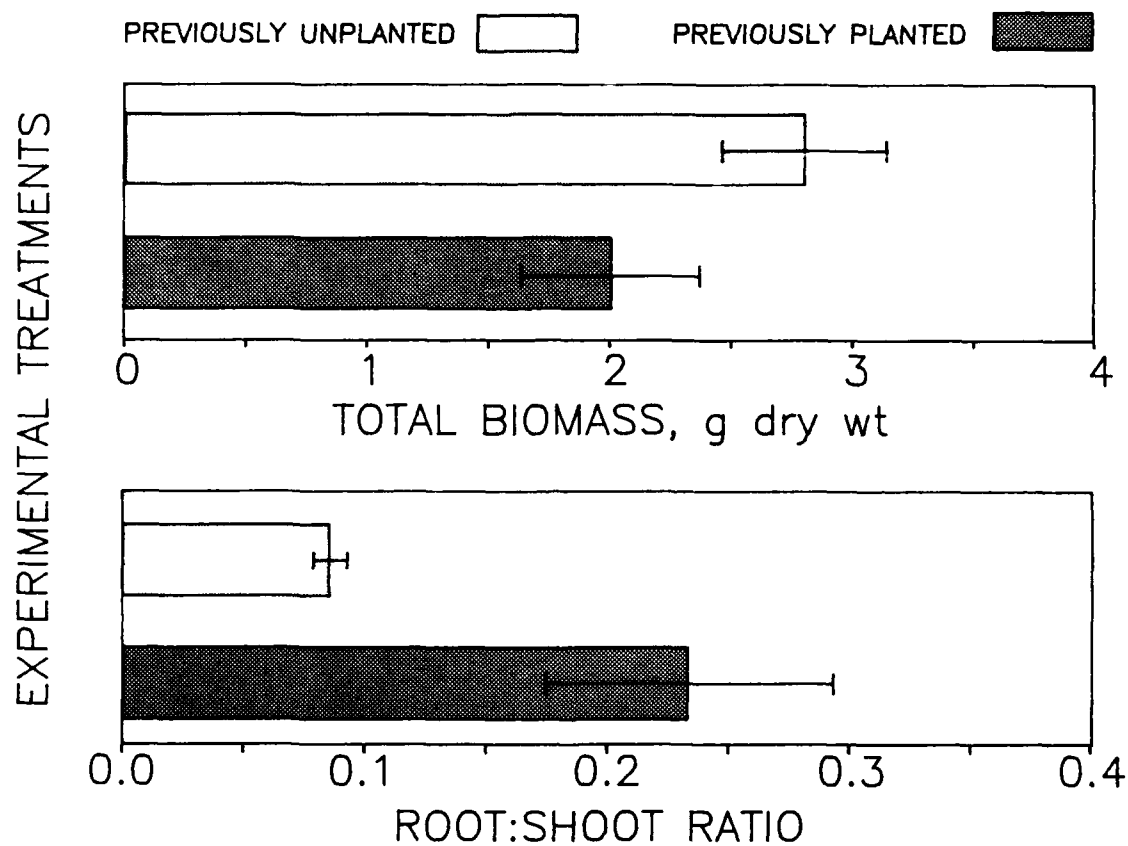


Figure 3. Total biomass production and the ratio of root to shoot biomass in *Hydrilla* grown on previously planted and previously unplanted sediment. Horizontal bars represent means ($n = 6$), with associated standard deviations

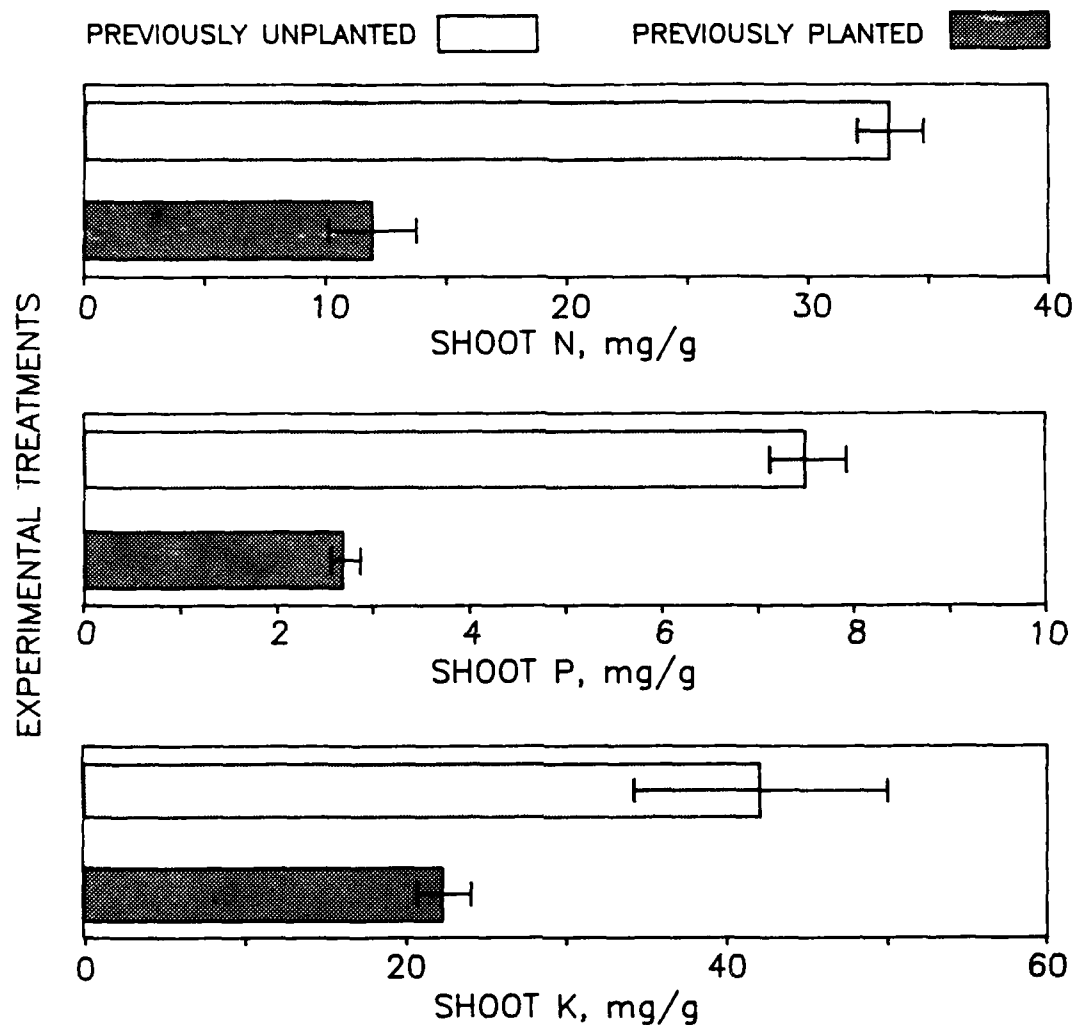


Figure 4. Shoot nutrient concentrations in *Hydrilla* grown on previously planted and previously unplanted sediment. Horizontal bars represent means ($n = 6$), with associated standard deviations

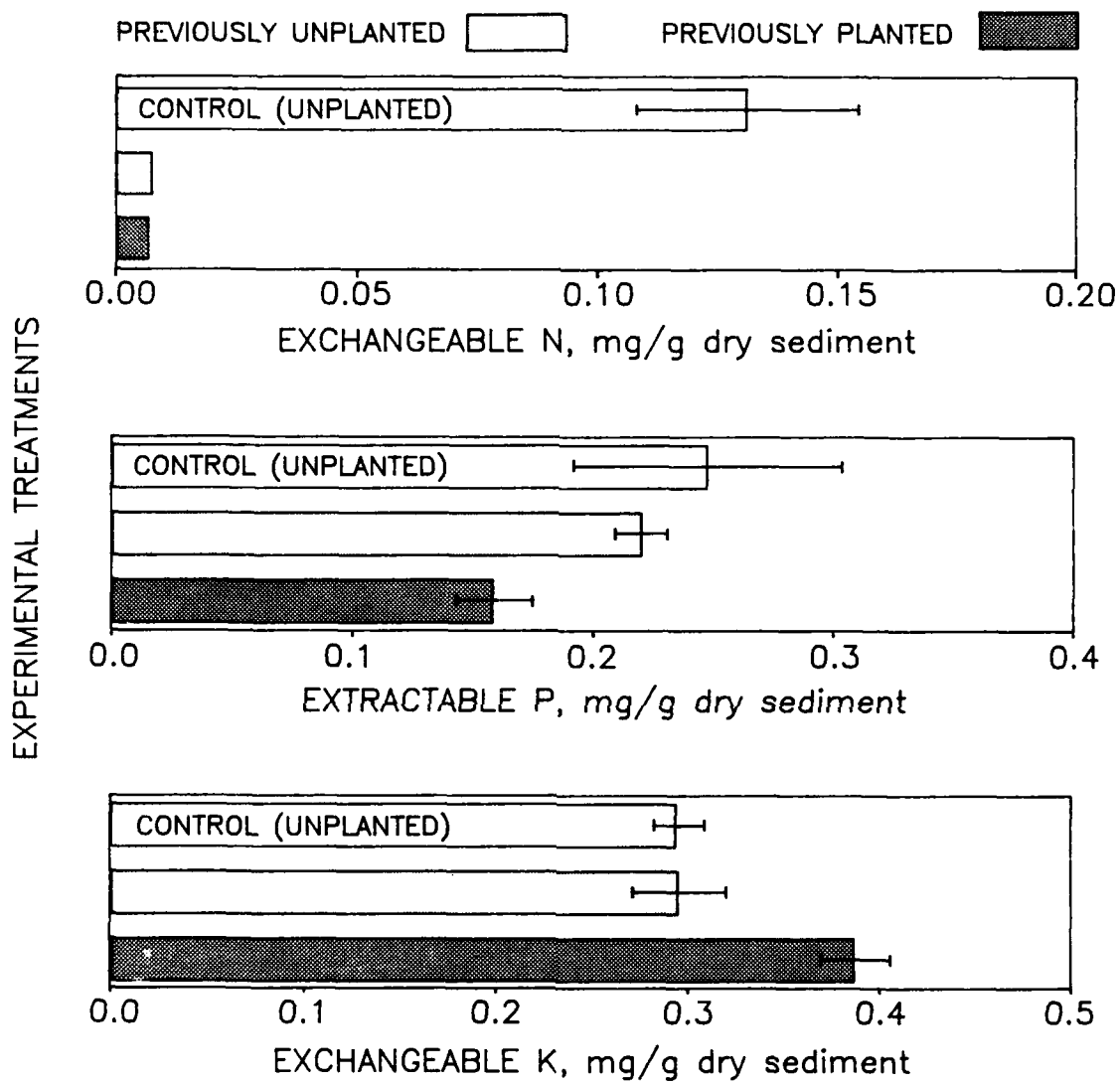


Figure 5. Concentrations of extractable sediment nutrients after one and two periods of *Hydrilla* growth in relation to concentrations in control (unplanted) sediment. Horizontal bars represent means ($n = 3$), with associated standard deviations

However, there was a much smaller pool of nutrients in the interstitial water than associated with sediment exchange sites. On the whole, changes in nutrient masses determined in the interstitial water were less than 15 percent of respective changes determined in sediment extracts.

16. Losses of nutrients from the control sediment over the duration of the study (both phases) due to nonplant-related processes (diffusion, advection, etc.) accounted for decreases in mass of extractable N, P, and K on the order of about 24, 26, and 8 percent, respectively. These losses were most significant during the second phase of study, and seemed to be associated with increased burrowing activity of benthic oligochaetes. In nutrient mass balance calculations, it was assumed that these losses occurred equivalently in planted and unplanted sediments.

17. In sediment following a single period of *Hydrilla* growth, measured decreases in mass of exchangeable N and extractable P (relative to the control sediment) were nearly identical to the accumulation of respective nutrients in *Hydrilla* shoots (Table 1). In marked contrast, the mass of exchangeable K was unaffected by a single period of planting, despite considerable accumulation of this element in *Hydrilla* shoots. During growth on previously planted sediment, the only treatment in which a net change in exchangeable K concentration occurred (Figure 5), the mass of exchangeable K in sediment increased by 69.2 mg, while 45.0 mg K was incorporated in *Hydrilla* shoots. In this treatment, there was considerable disparity between N and P accumulated in shoots and changes in respective nutrients in sediments. Most notably, 24.0 mg N accumulated in shoots with no measured change in exchangeable N concentration.

Secondary Studies

18. An association here between very low shoot N concentration in *Hydrilla* following growth on previously planted sediment (Figure 4) and a concomitant increase in concentration of exchangeable K in sediment (Figure 5) prompted the conduct of a secondary study to examine more fully the interactions between shoot N and exchangeable K concentrations. Over an 8-week period, exchangeable K concentration in unplanted Lake Washington control sediment remained statistically unchanged, while exchangeable K in the same sediment planted with *Hydrilla* increased significantly (Figure 6).

Table 1
Mass Changes in Extractable Sediment Nutrients and Nutrient
Accumulation in *Hydrilla* Shoots Following
One 6-Week Planting Period

Nutrient	Change in Sediment mg/container*	Accumulation in <i>Hydrilla</i> Shoots mg/container
N	-91.5	+92.4
P	-20.0	+21.0
K	+0.1	+117.6

Note: Values are means, calculated as products of shoot or sediment mass and nutrient concentration, determined from sediment extracts (n = 3) or shoot tissue digestates (n = 6).

* Negative values indicate net loss, while positive values indicate net accumulation.

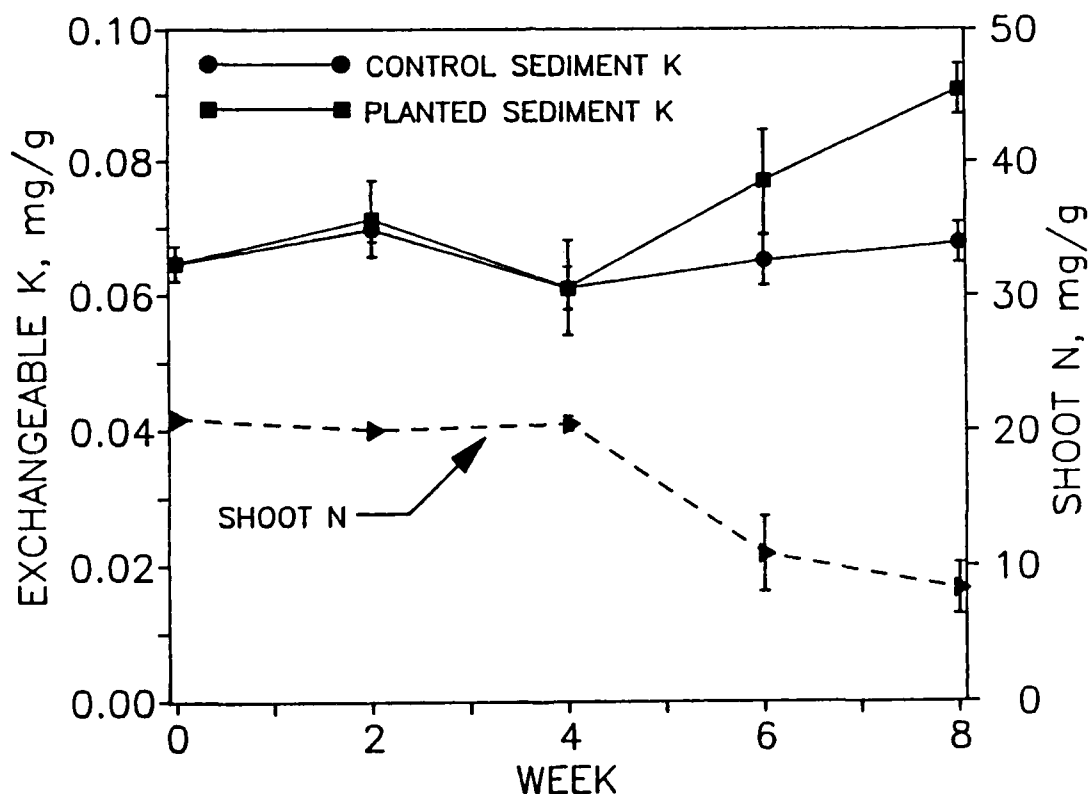


Figure 6. Relationship between exchangeable K concentration in planted sediment (relative to unplanted control) and concentration of N in *Hydrilla* shoots during an 8-week period of growth. Values of nutrient concentration are means (n = 4) with associated standard deviations

Increase in sediment K occurred between 4 and 8 weeks, and coincided precisely with significant decrease in shoot N concentration to very low levels. Increase in exchangeable K concentration followed a significant decrease in exchangeable N concentration in sediment to a very low level (<0.03 mg/g).

19. The possibility that some of the changes in nutrient content of planted sediments may have been facilitated by altered redox potential prompted the conduct of an additional study to examine interrelationships among macrophyte growth, sediment redox potential, and sediment nutrient composition. In this study, conducted over a 6-week period, biomass accrual (corrected for initial mass) in *Sagittaria* was about 2.5-fold greater than in *Hydrilla* (Figure 7). In *Hydrilla* nearly all of the biomass produced was in shoots, since roots comprised less than 2 percent of total biomass at 6 weeks. In contrast, root biomass in *Sagittaria* comprised about 30 percent of its total biomass at study end. Growth of *Hydrilla*, with minimal root mass, did not appreciably affect the vertical distribution of sediment redox potential relative to conditions in unplanted sediment; however, growth of *Sagittaria*, with a relatively massive root system, resulted in substantial oxidation of both sediments (Figure 8). Despite large differences between these species in both biomass accrual and effects on sediment redox potential, their influences overall on sediment nutrient composition were quite similar (Figure 9). After 6 weeks of growth, both species depleted exchangeable N concentrations to minimal levels and, as observed in the principal study (Figure 5), had a relatively minor influence on extractable P concentrations.

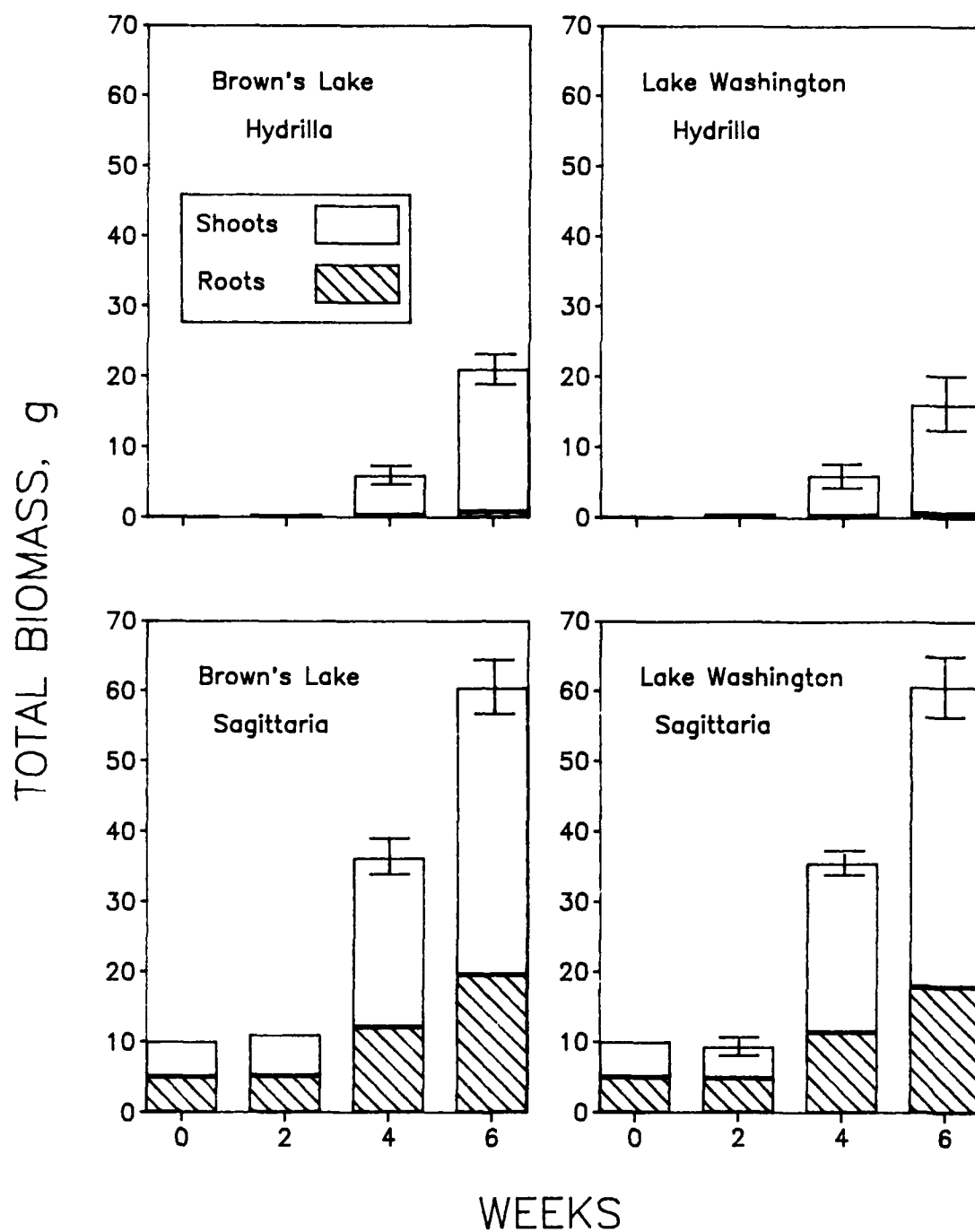


Figure 7. Total biomass production in *Hydrilla* and *Sagittaria* grown on Brown's Lake and Lake Washington sediments over a 6-week period. Vertical bars represent means ($n = 3$), with associated standard deviations

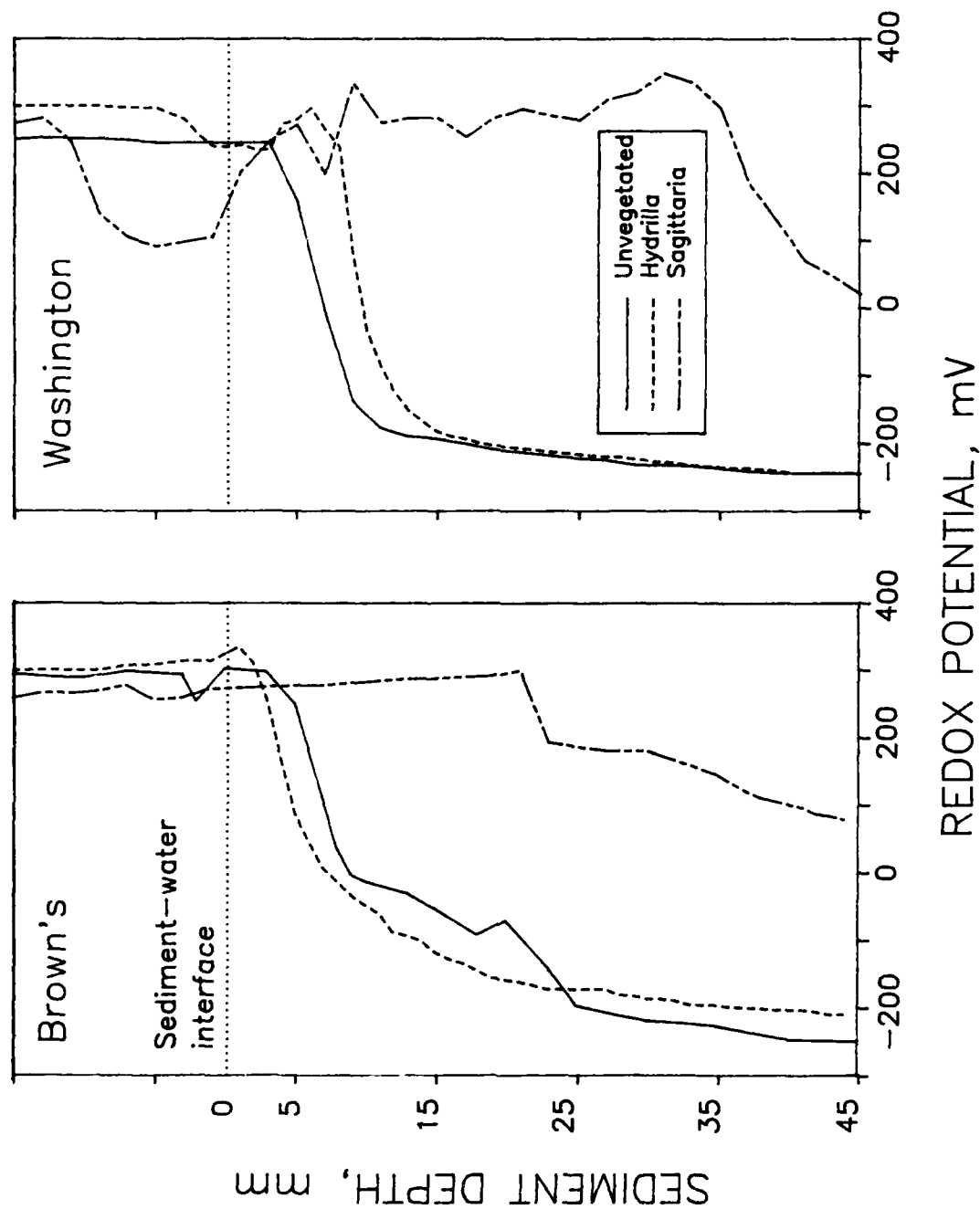


Figure 8. Comparisons of redox potential in planted and unplanted Brown's Lake and Lake Washington sediments after 6 weeks of *Hydrilla* and *Sagittaria* growth

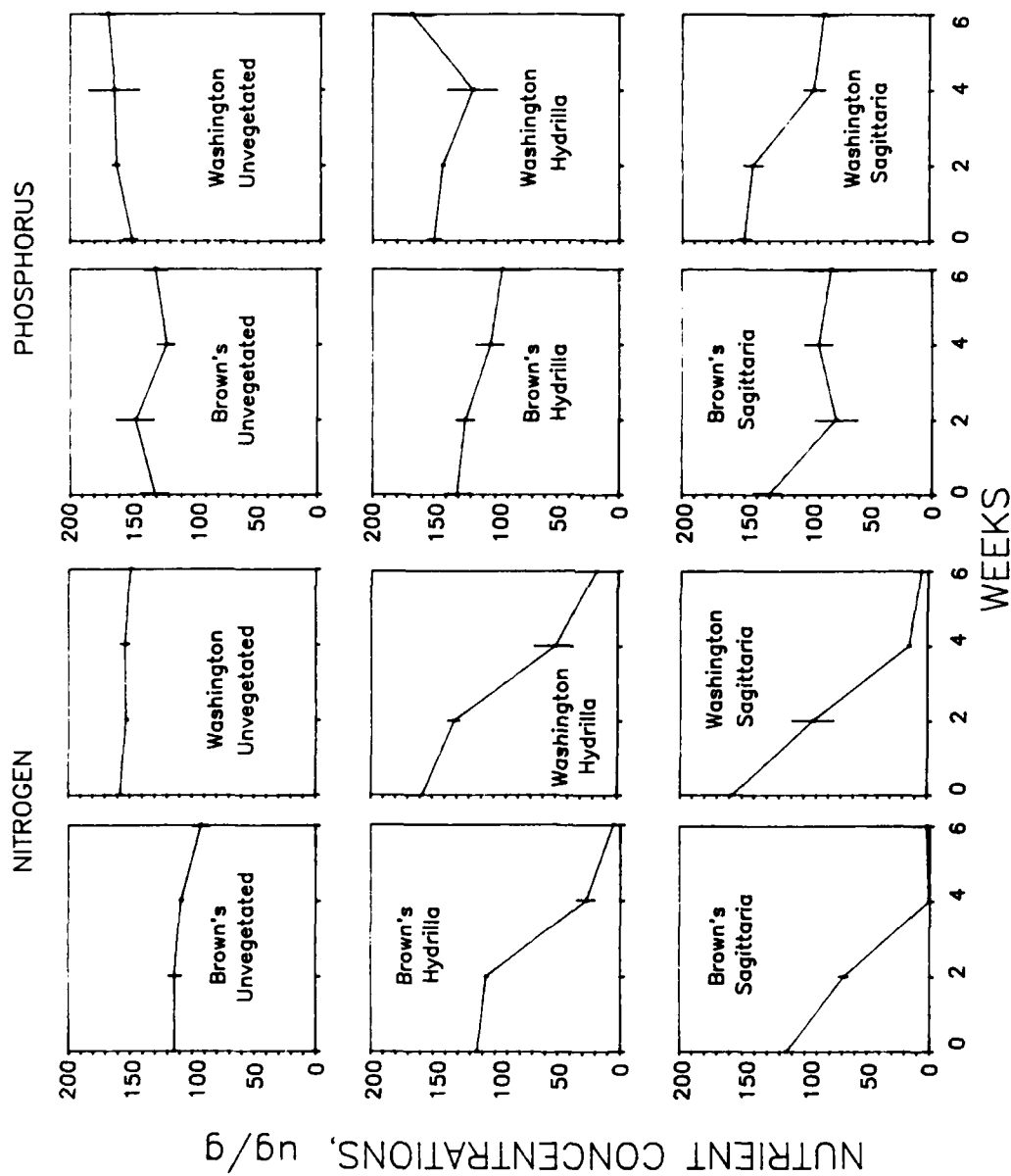


Figure 9. Changes in concentrations of exchangeable N and extractable P in planted and unplanted Brown's Lake and Lake Washington sediments over a 6-week period of *Hydrilla* and *Sagittaria* growth. Values of nutrient concentration are means ($n = 3$), with associated standard deviations

PART IV: DISCUSSION

20. Sediment nutrient availability has been demonstrated to greatly influence the growth of both freshwater (Barko and Smart 1986) and marine (Short 1987) vascular macrophytes. In the principal study, growth, morphology, and nutrient uptake in *Hydrilla* were substantially affected by changes in sediment properties induced by prior *Hydrilla* growth. Diminished growth of *Hydrilla* was associated primarily with autogenic reductions in exchangeable N concentration. From the general criteria of Gerloff (1975) and the authors' experience with *Hydrilla* (Barko 1982, Barko and Smart 1986), it is unlikely that the availability of P or K limited growth in any phase of these studies. However, on previously planted sediment in the principal study and after 6 weeks on sediment planted once in the secondary studies, very low values of shoot N concentration (<12.0 mg/g) indicate strongly that the growth of *Hydrilla* was limited by the availability of N. The increased ratio of root to shoot biomass in *Hydrilla* noted in this study on previously planted sediment is characteristic of diminished sediment fertility (cf. Denny 1980, Barko and Smart 1986).

21. Sediment clearly served as a source of N and P for *Hydrilla* in this investigation, but as a sink for K. Similar findings were reported by Carignan (1985) for *Myriophyllum spicatum* L. in Lake Memphremagog, where pronounced decreases in ammonium-N and P, in conjunction with increased K, were observed in the sediment interstitial water. Although exchangeable K was not measured in the study of Carignan (1985), increase in interstitial water K concentration was interpreted as a result of K displacement from sediment exchange sites. In the present investigation, increases in K concentration were observed in both sediment exchange sites and in the interstitial water. Thus, the findings of this study do not support desorption of K from ion exchange sites in sediment as a source for K increase in the interstitial water. Alternatively, it is suggested that the increase in sediment K resulted from transport of K from the overlying water, which has been identified as the primary source for K uptake by submersed macrophytes (Barko 1982, Huebert and Gorham 1983). Unpublished data from our laboratory indicate that between 30 and 60 percent of the K removed from solution in some of our laboratory studies cannot be accounted for by shoot tissue analysis; this may also represent K transported by submersed macrophytes to sediment.

22. Great differences in root versus shoot concentrations of K suggest a translocation gradient from shoots to roots in *Hydrilla* (Barko 1982). Since ammonium and potassium ions have the same charge and nearly identical ionic radii, it is possible that they compete for ion exchange sites. By saturating sediment exchange sites with K ions, rooted submersed macrophytes may effect an increase in sediment ammonium-N availability. From our analysis of the temporal relationship between shoot N status and concentrations of exchangeable K in sediment, it appears that sediment K accumulation occurs only when macrophyte growth becomes limited by the availability of N. Here it should be pointed out that the growth of *Myriophyllum* in Lake Memphremagog has been reported to be limited by N availability (Anderson 1985) among other possible factors (Duarte and Kalff 1986). Thus, K accumulation in the interstitial water of sediments reported by Carignan (1985) may have resulted from conditions of macrophyte N limitation. We postulate that, under N limiting conditions, K absorbed from the overlying water by macrophyte shoots is translocated to roots where it is exchanged for ammonium ions in sediment, thus potentially increasing availability of N.

23. Removal of N and P from sediment by *Hydrilla*, calculated here on the basis of either measured accumulation in shoots or respective decrease from sediment relative to control during a single 6-week planting (Table 1), amounted to 9.2 and 2.1 g/m² of sediment surface area, respectively. Nutrient removal from sediment planted with *Hydrilla* (corrected for diffusional losses) in this investigation appears to have been almost entirely a function of nutrient uptake, since this species had only a minor influence on sediment redox potential. Changes in the nutritional composition of sediment planted with *Sagittaria* also appear to have been due primarily to uptake, despite its demonstrated ability to oxidize sediment.

24. Sediment oxidation by aquatic macrophytes can enhance P retention, due to altered equilibria between phosphorus pools in sediment and overlying water (Jaynes and Carpenter 1986). In addition, oxidative processes occurring at the root/sediment interface may promote losses of N due to nitrification (Reddy and Patrick 1984). These processes are undoubtedly operational, but their impact on sediment chemistry can be expected to vary with differences in the oxygen-transporting capacity of aquatic macrophyte species (Sand-Jensen, Prah1, and Stockholm 1982). Species such as *Sagittaria*, which can

significantly modify sediment redox potential, may have an effect on sediment nutrient composition exceeding that due to nutrient uptake alone.

25. Smith and Adams (1986) estimated that *M. spicatum* in Lake Wingra during 1977 removed P from sediment at a rate of $2.2 \text{ g/m}^2/\text{year}$, similar to our estimate for *Hydrilla* determined during a single 6-week planting period in the laboratory. In a related investigation, Prentki (1979) provided evidence that over a 21-year period of submersed macrophyte existence in Lake Wingra, an average of $1.4 \text{ g P/m}^2/\text{year}$ was lost at root depth from the sediment profile. Prentki (1979) and Smith and Adams (1986) considered P losses from vegetated littoral sediments in Lake Wingra to be greatly in excess of sedimentation of P in "available" forms. Equivalent information is not available for nitrogen; however, Short (1983) reported a substantial decrease in the interstitial ammonium pool of sediment over a 4-year period of colonization by the seagrass *Zostera marina* L. Results of our investigation, in combination with consideration for shoot nutrient stoichiometry (Filbin and Barko 1985), suggest that losses from sediment of available N due to uptake by rooted submersed macrophytes may actually be greater than losses of P.

26. Given the potential of rooted macrophytes to deplete sediment nutrient pools, it is important to better understand sources and mechanisms of nutrient replenishment. Sedimentation, perhaps the most significant mechanism of nutrient replenishment, is enhanced in aquatic macrophyte beds, since they serve as effective traps for inflowing dissolved and particulate materials (Wetzel 1979, Carpenter 1981). It has been speculated that nutrient deposition associated with sedimentation may be an important determinant of species composition and successional development in aquatic macrophyte communities (Carpenter 1981; Barko and Smart 1983, 1986). Macrophyte species, with a propensity during growth and senescence for large losses of nutrients, probably impose greater demands on sediment nutrient reserves over the long term than nutritionally more conservative species. Thus, variations in the capacity of different aquatic macrophyte species both to deplete sediment nutrients and to contend with autogenic reductions in sediment nutrient availability may have, in addition to sedimentation, an important influence on successional development in aquatic macrophyte communities.

27. Nutrients in the root zone of aquatic macrophytes may be redistributed by chemical diffusion and by the activities of benthic invertebrates (e.g., Fukuhara and Sakamoto 1987). Effects of bioturbation on sediment

properties have been investigated in some detail (e.g., McCall and Fisher 1980), but not within the context of aquatic macrophyte nutrition. The microbial community of sediments appears to play a key role in nutrient replenishment within aquatic macrophyte beds (Craven and Hayasaka 1982; Boon, Moriarity, and Saffigna 1986). Mineralization of organic matter from macrophyte roots was demonstrated to be an important source of nitrogen to submersed macrophytes in Lake Memphremagog (Carigan 1985), and in our laboratory investigation may have been the only source of N available to *Hydrilla* grown on previously planted sediment.

28. Because they link sediment and overlying water, submersed macrophytes potentially have significant effects on sediment-water biogeochemical interactions (Carpenter 1983; Carpenter and Lodge 1986; Lodge et al., in press). These effects may be due directly to nutrient uptake as evidenced here, or indirectly to metabolic transformations of sediment nutrient pools, as evidenced in the study of Jaynes and Carpenter (1986) and discussed above. Overall, in the field of aquatic ecology, far greater attention has been directed toward sediment properties affecting macrophyte growth than toward the effects of macrophyte growth on sediment properties. From results of this investigation it is apparent, however, that these effects are reciprocally interactive. Better elucidation of macrophyte effects on sediment properties will be necessary to extend current understanding of the nutritional ecology of submersed macrophytes to a more holistic understanding of biogeochemical interactions in aquatic systems.

PART V: CONCLUSIONS AND RECOMMENDATIONS

29. The growth of *Hydrilla* can be significantly retarded on sediment subjected to previous macrophyte growth. Reduced growth under these conditions is a result of progressive nutrient deficiency imparted by prior nutrient uptake. Based upon results of this laboratory study and referenced field studies, it appears that nutrient uptake from sediment by submersed aquatic macrophytes can exceed nutrient replenishment in littoral zones. Sedimentation is likely to be the dominant mechanism of nutrient replenishment in most aquatic systems. Therefore, it is reasonable to postulate that reductions in sediment loadings may eventually result in decreased productivity of rooted submersed aquatic vegetation. It is, of course, also possible that other mechanisms of nutrient replenishment (e.g., diffusion, advection, mineralization, fixation, bioturbation, etc.) in littoral sediments are also operational in maintaining macrophyte productivity. These mechanisms, within the context of aquatic macrophyte nutrition, have been investigated in some detail in marine systems, but have been largely ignored in freshwater systems. The sustained vigor of rooted submersed macrophyte communities will depend, among other factors, on the balance between nutrient losses and gains in littoral sediments. In this regard it is important to better understand mechanisms affecting this balance.

30. From results of this and past studies in our laboratory, it appears that nitrogen is a key element in sediment, often limiting the growth of rooted aquatic macrophytes. The exchange of K for ammonium-N in sediment, identified here in *Hydrilla* as a potential means of coping with N limitation, is a novel finding. However, the extent to which this exchange process is operational in other aquatic macrophytes is unknown. This process could be unique to only certain macrophyte species, in which case they might have a competitive advantage under N-limiting conditions. Accordingly, it is recommended that these exchange relationships be examined in a broad variety of exotic as well as native macrophyte species. Additionally, it is important to determine the extent to which nutrition, among other factors affecting macrophyte growth, bears on competitive interactions that ultimately dictate macrophyte community composition.

31. This investigation reinforces results of earlier studies, conducted at the WES, which have indicated strong relationships between sediment

composition and aquatic macrophyte growth. It is now apparent that sediment composition is as much a product of macrophyte growth as it is a delimiter of macrophyte growth. Future investigations of the feasibility of lessening sediment nutrient availability by chemical means, or perhaps by selective macrophyte harvesting and replanting, need to be conducted; these will be valuable in broadening the scope of aquatic plant management in freshwater systems.

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